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ORGANISMIC REMOTE SENSING FOR TROPICAL FOREST ECOLOGY AND CONSERVATION[1,2]

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Abstract

Tropical forests are vast and scientifically underexplored places. Biotic losses, gains, and reorganization within these systems go undetected due to a lack of access to technologies needed to monitor forest cover, composition, and carbon content. Provision of forest cover-monitoring tools for non-scientists has, thus, become a focus of innovation in the remote-sensing community, while advances in high-resolution forest carbon and biodiversity mapping science has progressed more slowly. This paper focuses on high-resolution remote-sensing developments to measure and monitor tropical forest canopies at the "organismic scale," which is the resolution that resolves individual canopies and species throughout the forest landscape. Emphasis is placed on how forest carbon stocks can be mapped with precision and accuracy comparable to that of field-based estimates. Biodiversity mapping poses the greatest challenge, but recent advances in three-dimensional functional and structural trait imaging can reveal variation in species richness, abundance, and functional diversity over large geographic regions. The pay-off in pursuing these studies will be a vastly improved understanding of tropical biodiversity patterns and their underlying ecological and evolutionary drivers, which will have positive cascading effects on conservation decision-making and resource policy development.

Key words: Biodiversity, canopy chemistry, Carnegie Airborne Observatory (CAO), conservation, functional diversity, LiDAR, rainforest, tropical forest.

Introduction

Following four billion years of evolution on Earth, the most biologically diverse biome to have arisen on land is the great swath of tropical forest straddling the equator. However, tropical forests continue to undergo losses and biotic rearrangement in complex spatial patterns and at variable rates that defy most conservation policy initiatives (Venter et al., 2013; Lindenmayer et al., 2014). Despite the importance of the tropics, a plethora of barriers exist to the effective monitoring of changes in forest cover and composition at large enough geographic scales, and with the required spatial detail, to create transparent infor-

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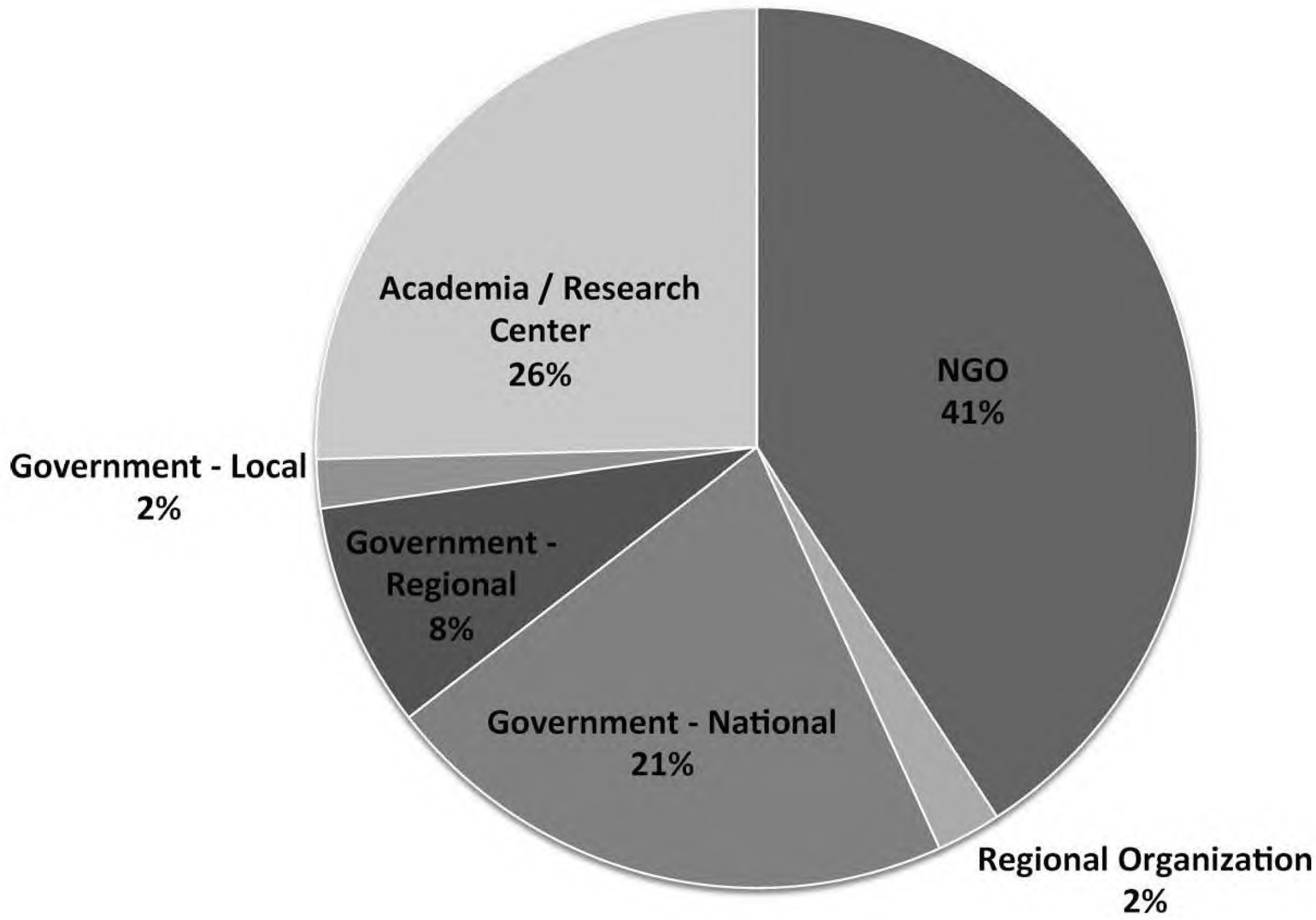


Figure 1. The distribution of the CLASlite deforestation and forest degradation mapping community in Latin America (among 1700 organizations as of August 2014). NGO is a non-government organization within any given country. A regional organization is one that operates in two or more countries.

mation for the management and conservation of this exceptional biome. What are the barriers, and how do we break them down?

In terms of forest cover monitoring, including deforestation and forest degradation, a persistent problem has been the inaccessibility of straightforward satellite-based technology. For years, the Brazilian Institute for Space Research has led the way toward removing this barrier, with a state-of-the-art deforestation monitoring system for the Brazilian Amazon (Instituto Nacional de Pesquisas Espaciais [National Institute for Space Research; INPE], 2007). Now a parallel system operated by the Brazilian non-government organization IMAZON (<http://imazon.org.br>) monitors both deforestation and forest degradation. Several other monitoring systems are also operated by experts (reviewed by Achard et al., 2007), providing national to global-scale estimates of deforestation, albeit with degradation rarely included (Global Observation of Forest and Land Cover Dynamics [GOFC-GOLD], 2008). In many cases, the forest change maps are being actively disseminated, and these efforts demonstrate that vast regions of tropical forest cover can be monitored. However, a growing number of stakeholders want to conduct their own monitoring, so providing access to the technology has recently become a focus of innovation in the mapping sciences.

To address this challenge, some groups are making the techniques, software, and support available for non-experts wishing to monitor forest cover. The Carnegie Institution's system, called CLASlite, was designed to provide the tools for monitoring deforestation and forest degradation directly to the end-user (Asner et al., 2009b). CLASlite is based on the original Carnegie Landsat Analysis System (CLAS; Asner et al., 2005, 2009d; Oliveira et al., 2007; Broadbent et al., 2008), and it has been used to map changes in forest cover and disturbance in various regions of the world (e.g., Carlson et al., 2012; Allnutt et al., 2013; Carvalho et al., 2013). Supporting input from eight different satellites, CLASlite also helps users overcome some, but not all, problems of access to data derived from otherwise hard-to-use satellite imagery. The system runs on a standard personal computer and has been actively disseminated to users in more than 1700 organizations in over 120 countries throughout the world (Fig. 1; <http://claslite.ciw.edu>). Deforestation Alert System (Sistema de Alerta de Desmatamento; <http://imazon.org.br>) and other systems (Hansen et al., 2013) are also coming online via Google's Earth Engine (<http://earthengine.google.com>), which is giving users around the world access to free forest cover-monitoring tools. These and other initiatives suggest that monitoring forest cover is both technically tractable and on the rise institutionally.

Despite these advances in monitoring tropical forest cover, it is clear that we must also continue to seek ways to map what lies within tropical forests, including the canopy, carbon content, and biodiversity in terms of species presence, abundance, richness, and their functional traits. The need for

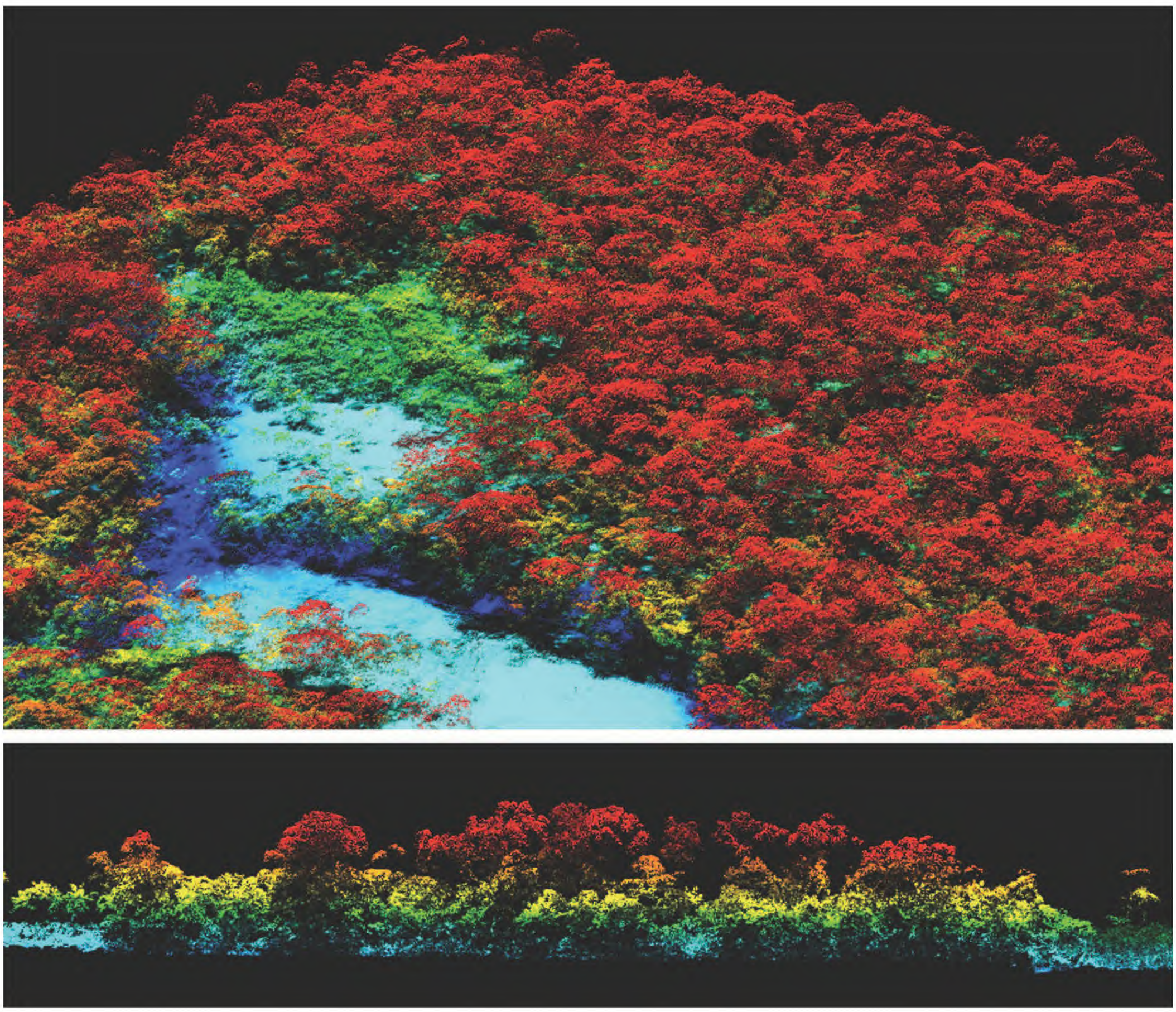


Figure 2. Airborne Light Detection and Ranging (LiDAR) provides three-dimensional imaging of ecosystems by measuring precise distances between ground and vegetation elements including foliage and woody stems. LiDAR works by sweeping a high-pulse rate laser outward from the bottom of an airplane, recording the elapsed time between laser pulses and returns. The upper image of the lowland Amazonian forest in Colombia was collected by the Carnegie Airborne Observatory (CAO; <http://cao.ciw.edu>) and is color-coded by height above ground as shown in the lower sectional view. Red indicates taller portions of the canopy; blue indicates shorter portions of the canopy.

tropical forest carbon monitoring has arisen throughout the conservation and climate-change communities, particularly as voluntary markets have provided project-level funds to protect forests based on carbon offsets (Parker et al., 2009) and as policy development continues toward compliance carbon-offset regulations at international (United Nations Framework Convention on Climate Change [UNFCCC], 2009) and jurisdictional (Odigha, 2010) levels.

Tropical forest carbon stocks also express the outcome of myriad evolutionary, ecological, and environmental processes, and, thus, carbon mapping could enrich our understanding of these processes operating at multiple spatial and temporal scales. Meanwhile, biodiversity monitoring continues to grow in importance as scientists, conservationists, and decision-makers face the specter of land use and climate-induced shifts and losses of species and communities (Jetz et al., 2007; Williams et al., 2007; Hubbell et al., 2008; Malhi et al., 2009; Asner et al., 2010a). Yet, spatially explicit, high-resolution maps of carbon stocks and biodiversity rarely exist, and certainly not over extensive reaches of tropical forest. Why is that the case? High-resolution mapping science is only now figuring out how to get at the required measurements remotely, and some of the advances are too new for, or simply do not work with, more widely available satellite instrumentation (Schimel et al., 2013). In the remainder of this paper, I focus on some advances in mapping of tropical forest carbon stocks and composition at the "organismic

scale," that is, with detail resolving individual canopies and species throughout the forest landscape.

Forest Carbon

Maps of tropical forest carbon stocks have traditionally relied upon field inventory plots, in which stem diameters and estimates of canopy height are measured and recorded by hand (USDA Forest Service, 2008). The problem posed by this traditional inventory approach is that it requires a dense array of plots in order to characterize different types of forest, forest conditions including different ages of secondary regrowth, forests of varying levels of degradation, and environmental controls over spatial patterns in carbon stocks. The number of plots required to meet this need is often dizzying from both logistical and financial standpoints. Additional resources are, therefore, needed to decrease the reliance on field plots and to provide spatially contiguous data that will support initiatives to reduce carbon emissions from tropical forests.

Developing high-resolution carbon maps requires measuring forest stocks as accurately as field plots, while also sampling over large, continuous gradients of climate, topography, hydrology, soils, and biological diversity. The measurements must also resolve highly variable effects of land use on carbon stocks. A major new contributor to solving the carbon mapping challenge is airborne Light Detection and Ranging (LiDAR), a technology that images forest canopies in three dimensions using emitted laser light pulses (Lefsky et al., 2002b; Mascaro et al. 2014) (Fig. 2). When calibrated to on-the-ground carbon stocks, LiDAR has provided high-resolution, spatially contiguous estimates of aboveground carbon throughout tropical landscapes (Drake et al., 2002a, 2002b; Lefsky et al., 2002a; Clark et al., 2011).

Airborne LiDAR-derived maps of tropical forest carbon have proven increasingly precise and accurate, with errors comparable to those derived from field plots (Mascaro et al., 2011b). Tropical forest field plots based on traditional allometric equations produce errors in the 10%–25% range (Keller et al., 2001; Chave et al., 2004; Alves et al., 2010); the prediction errors inherent in using LiDAR are now well within that range, hovering around 10%–13% compared to estimates based on exhaustively measured field plots (Asner et al., 2012c; Zolkos et al., 2013). Although LiDAR can be expensive to use over small project areas, there is a large economy-of-scale effect that can reduce its cost to less than US 10¢ per hectare in larger projects (Asner et al., 2010b, 2012a). As plot-based estimates continue to improve, LiDAR-based estimates will also advance to greatly extend the limited spatial density and geographic extent of tropical plot networks.

Research in the airborne LiDAR arena has demonstrated the tractability of tropical forest carbon mapping at large geographic scales of thousands to millions of hectares. High-resolution LiDAR-based maps are particularly useful because other field- and map-based ecological data can be integrated with them. This has afforded the opportunity to study how environmental and land-use factors influence forest structure and carbon stocks, and how these controls may be tied to gradients in biological diversity. For example, Mascaro et al. (2011a) found that topographic slope was positively correlated with aboveground carbon stocks on Barro Colorado Island in the Republic of Panama. Based on other studies, the LiDAR findings also suggest that erosional surfaces on or at the foot of hillslopes, which often harbor soils of locally higher fertility compared to topographic crest areas (Porder et al., 2005; John et al., 2007) and which can be associated with unique species compositions in some forests (Clark et al., 1999), may result in elevated carbon stocks. Combining LiDAR and hyperspectral remote-sensing data in Hawaiian rainforests, Asner et al. (2009a) developed a similar set of topographically mediated results but also resolved the effects of species on carbon storage. Carbon was found to vary with slope, elevation, and soil age, and the imprint of species on carbon stocks trumped climate and fertility gradients by up to 300%. This approach, combined with satellite data on forest cover and deforestation, subsequently provided a means to map the effects of environment, humans, and other species on carbon stocks throughout Hawai'i (Asner et al., 2011b) (Fig. 3). These and other studies reveal underlying controls on forest carbon, indicating functional processes as well as impacts of human activities.

Canopy Diversity

While high-resolution forest carbon monitoring has advanced at a rapid pace, parallel undertakings with biodiversity mapping have proven more challenging. Rather than focusing on the better-established role of remote sensing in determining broad-scale aspects of biodiversity, such as vegetation patch size, shape, and location, among others (Innes & Koch, 1998; Foody, 2003; Turner et al., 2003; Gillespie et al., 2008), here, the emphasis is on the richness and abundance of plant species and functional types within tropical forests. The focus is specifically related to the organismic scale that can discern individuals within the canopy, although some very innovative work linking medium-resolution (~30 m)

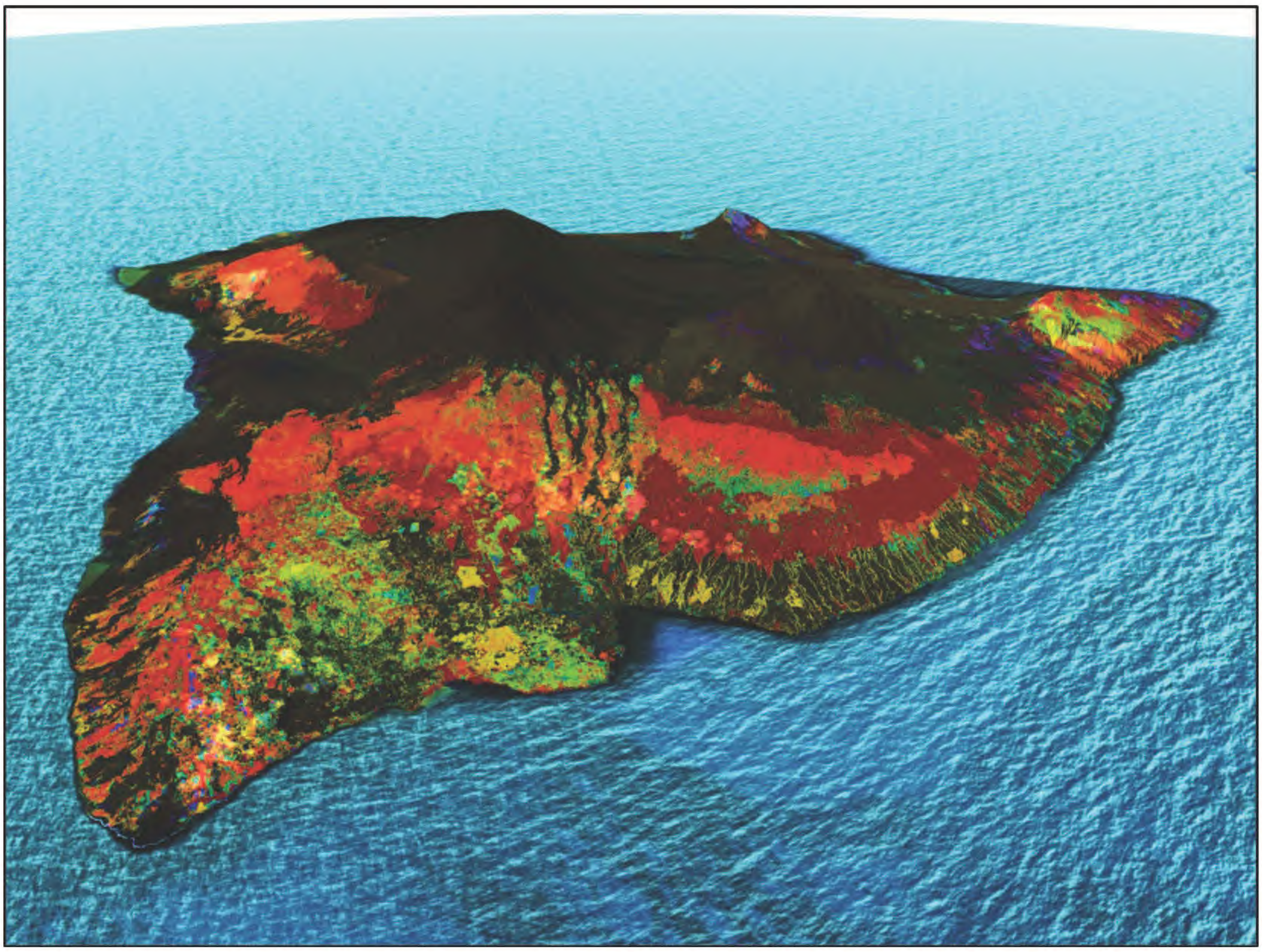


Figure 3. A first-time view of aboveground vegetation carbon stocks across the Island of Hawai'i, derived from airborne LiDAR and satellite data, draped over a digital elevation model. The regional distribution of carbon stocks shows high values in red (> 100 Mg C ha^{-1}) corresponding to humid tropical forests and plantations, and lows in purple (< 20 Mg C ha^{-1}) representing dry woodland vegetation. This map was created from data provided by Asner et al. (2011).

satellite metrics with biodiversity gradients should not be forgotten (Saatchi et al., 2008; Gillespie et al., 2009; Rocchini et al., 2010). Much of the work described in this section requires airborne data, although high-resolution (1–4 m) spaceborne images are also contributing to the effort (Hurtt et al., 2003; Read et al., 2003; Clark et al., 2004a; Palace et al., 2008).

The portion of forest diversity most accessible to organismic remote sensing is the canopy, and, thus, this is where mapping studies have naturally focused. Given the central role that canopies play in harboring all flora and fauna (Connell, 1978; Orians et al., 1996) and in mediating millions of interactions among the biota (Janzen, 1970), there is no doubt that mapping canopy diversity will transform the way that tropical ecosystems are studied. Clearly, mapping would also have a positive impact on tropical forest assessments used in conservation planning and policy development, since it would identify the location and extent of biodiversity gradients and hotspots.

The challenge with canopy-diversity mapping ultimately rests in identifying plant traits that indicate spatial variability among organisms and which of those traits can also be detected via remote sensing. Plant traits not only express variation in ecological processes (Wright et al., 2004; Ollinger, 2011), but also can be related to variation in species composition and phylogeny (Rees et al., 2001; Funk et al., 2008; Ackerly, 2009). With respect to remote sensing, the potential traits encompass functional characteristics, such as spectral and chemical properties, as well as canopy structural characteristics (Table 1). Spectral traits are those describing the reflectance, transmittance, and absorptance patterns at leaf and canopy levels. Chemical traits include a wide variety of compounds mediating light capture and growth, longevity, and defense (Asner et al., 2011c). Light capture-growth traits include photosynthetic pigments, such as chlorophylls and carotenoids, nitrogen, and phosphorus (Evans, 1989; Niinemets et al., 1999). Longevity and defense compounds include lignin and cellulose that are

Table 1. Some plant traits that have proven to be related to biological diversity and which are also accessible via remote sensing. Example references are provided, with an emphasis on tropical forests where possible.

Trait	Example references
Functional	
Spectral reflectance	Carlson et al. (2007), Ustin & Gamon (2010)
Light absorption	Avalos et al. (1999), Lucas & Carter (2008)
Chlorophylls	Castro-Esau et al. (2006), Sanchez-Azofeifa et al. (2009)
Carotenoids-anthocyanins	Blackburn (1998), Sims & Gamon (2002)
Leaf mass per area (LMA)	Poorter (2000), Asner et al. (2011e)
Nitrogen and phosphorus	Porder et al. (2005), Martin et al. (2008)
Base cations (Ca, Mg, K)	Asner & Martin (2011), Asner et al. (2011d)
Lignin, cellulose	Curran et al. (1997), Almeida & Filho (2004)
Phenols, tannins	Kursar et al. (2009), Skidmore et al. (2010)
Water	Asner et al. (2004), Clark et al. (2011)
Structural (canopy)	
Leaf area index (LAI)	Thenkabail et al. (2004), Gillespie et al. (2009)
Height	Drake et al. (2002b)
Crown diameter	Read et al. (2003), Clark et al. (2004a)
Crown depth	Clark et al. (2004b)
Vertical foliage profile	Weishampel et al. (2000), Asner et al. (2008a)

structurally tough (Melillo et al., 1982) as well as phenols and tannins that can be used against pests and pathogens (Coley et al., 1993). An example of an overarching or synthetic structural trait is leaf mass per area (LMA). Although not directly indicative of a chemical compound or element, LMA often correlates with growth and longevity chemistries (Wright et al., 2004; Poorter et al., 2009), and LMA has a strong role in determining the spectral reflectance properties of tropical canopies (Asner et al., 2011e). Canopy structural traits range from leaf area index (LAI), which is the total projected leaf area per unit ground area (Kira et al., 1969), to canopy height, crown diameter and depth, and the vertical distribution of foliage (Lefsky et al., 2002b).

Progress in canopy-diversity mapping has been made on several fronts, at times based explicitly upon the detection and interpretation of these plant functional and structural traits. Work in this arena can be partitioned into species richness, species detection, and functional diversity. Canopy richness is defined as the number of canopy species per unit area. From a remote-sensing perspective, richness mapping has not necessarily required that each species be identified. Instead the number of unique organisms per unit area can be detected based on spatial variation in traits. Studies show that this can be achieved either by directly associating spectral diversity with species richness, or by converting remotely sensed metrics to plant traits followed by classification of these traits to diversity estimates. A number of satellite studies have related optical and radar signals with spatial gradients in species richness (e.g., Foody & Cutler, 2003; Saatchi et al., 2008; Rocchini et al., 2010). However, at organismic scales, Carlson et al. (2007) first found that spectral diversity varies with species richness per unit area in lowland Hawaiian tropical forests (Fig. 4). Their work, like that of many others in this particular research area, utilized airborne imaging spectroscopy, which is composed of precisely co-located images in hundreds of narrow and contiguous spectral channels often spanning the 400–1050 nm (visible to near-infrared) or 400–2500 nm (visible to shortwave-infrared) wavelength range (Goetz et al., 1985; Asner et al., 2012d). A reflectance signal derived for each spectrometer image pixel then allows for detailed analysis using a wide variety of canopy spectral and chemical traits, summarized by Blackburn (2007), Kokaly et al. (2009), Ustin et al. (2009), and many others.

With imaging spectrometer data, Carlson et al. (2007) estimated species richness for very tightly packed canopies of up to 33 trees per 0.1 ha and found that richness levels were elevated in zones where native and invasive species intermix in communal areas outside of the few remaining protected areas that harbor lower diversity communities harboring highly endemic species. This type of airborne work has been mirrored in leaf-level studies of tropical forests, where increasing spectral diversity has been linked to biological diversity among canopy species in Panama (Castro-Esau et al., 2006) and elsewhere in Hawai‘i (Féret & Asner, 2011). Critically, these and other studies (e.g., Sanchez-Azofeifa et al., 2009) demonstrate that spectral diversity is a direct expression of leaf chemical diversity, particularly among the chemical elements

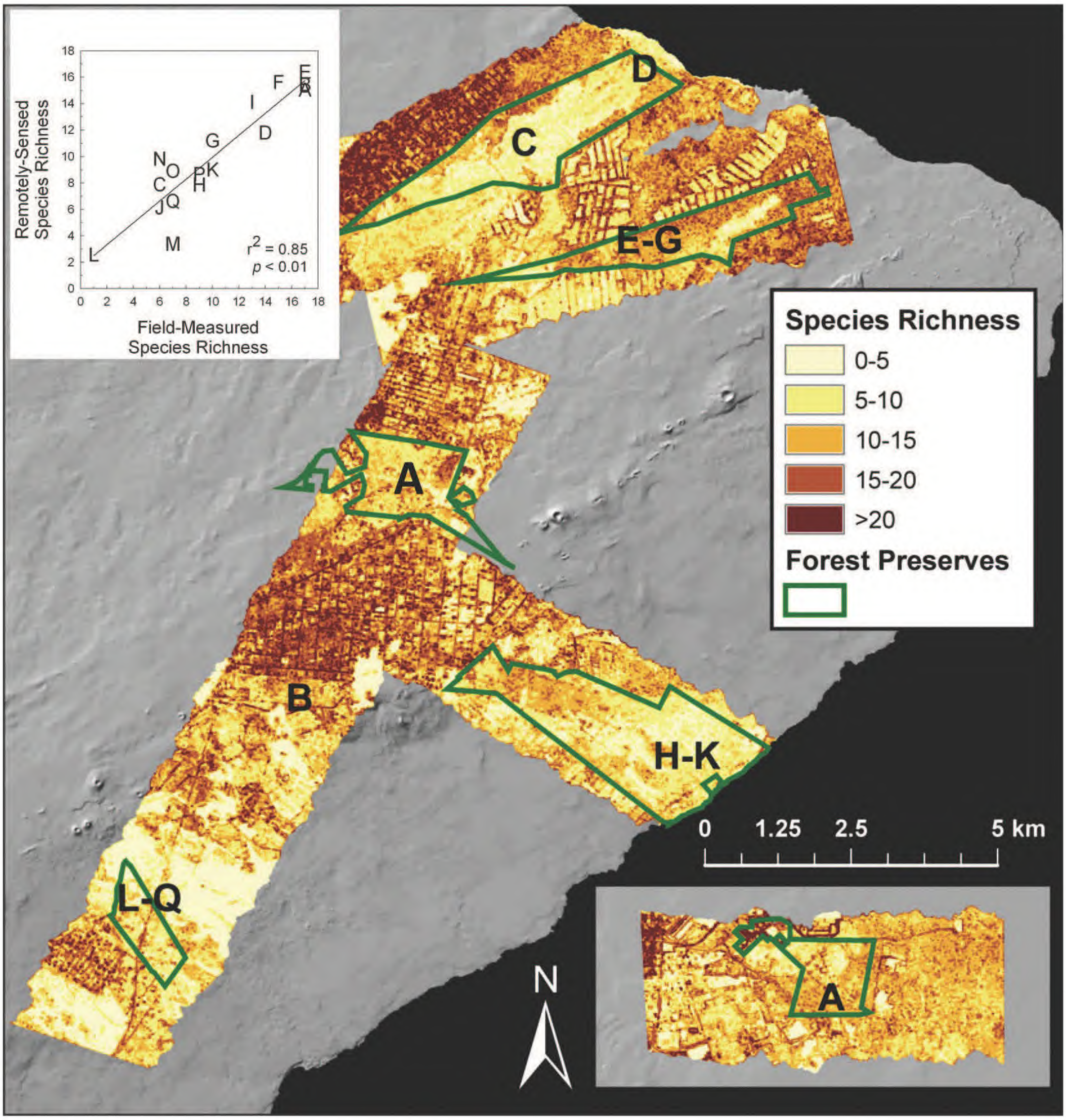


Figure 4. Maps of species richness (number of species per unit area) in lowland forests of the Puna District, Island of Hawai'i. In this set of examples, protected areas (green polygons) harbor relatively low-diversity native Hawaiian plant communities. Zones of higher species richness are found in communal areas harboring many exotic species. A–Q. Field validation sites as shown in the graph inset to the upper left. These maps were created using data from Carlson et al. (2007).

and compounds listed in Table 1. In general, spectral variance increases with chemical variance among co-existing organisms until an asymptote is reached (Asner & Martin, 2009). The saturation point at which adding organisms no longer leads to enhanced spectral or chemical variance is dependent upon the composition of an ecosystem, with climate and soils playing an important mediating role (Asner et al., 2009c; Féret & Asner, 2012b).

While species richness provides some insight into biological diversity, the holy grail of remote sensing is the ability to detect and map particular species (Innes & Koch, 1998; Nagendra, 2001; Turner et al., 2003; Saatchi et al., 2008). Aerial photographs have been used for years to estimate the cover and abundance of conspicuous temperate or plantation species (e.g., Swetnam et al., 1999), and some of that capability has been transferred to high-resolution spaceborne cameras (Thenkabail et al., 2004). Yet, standard imaging cameras have yielded little information on species distributions in tropical canopies. Detection of individual species depends almost entirely upon

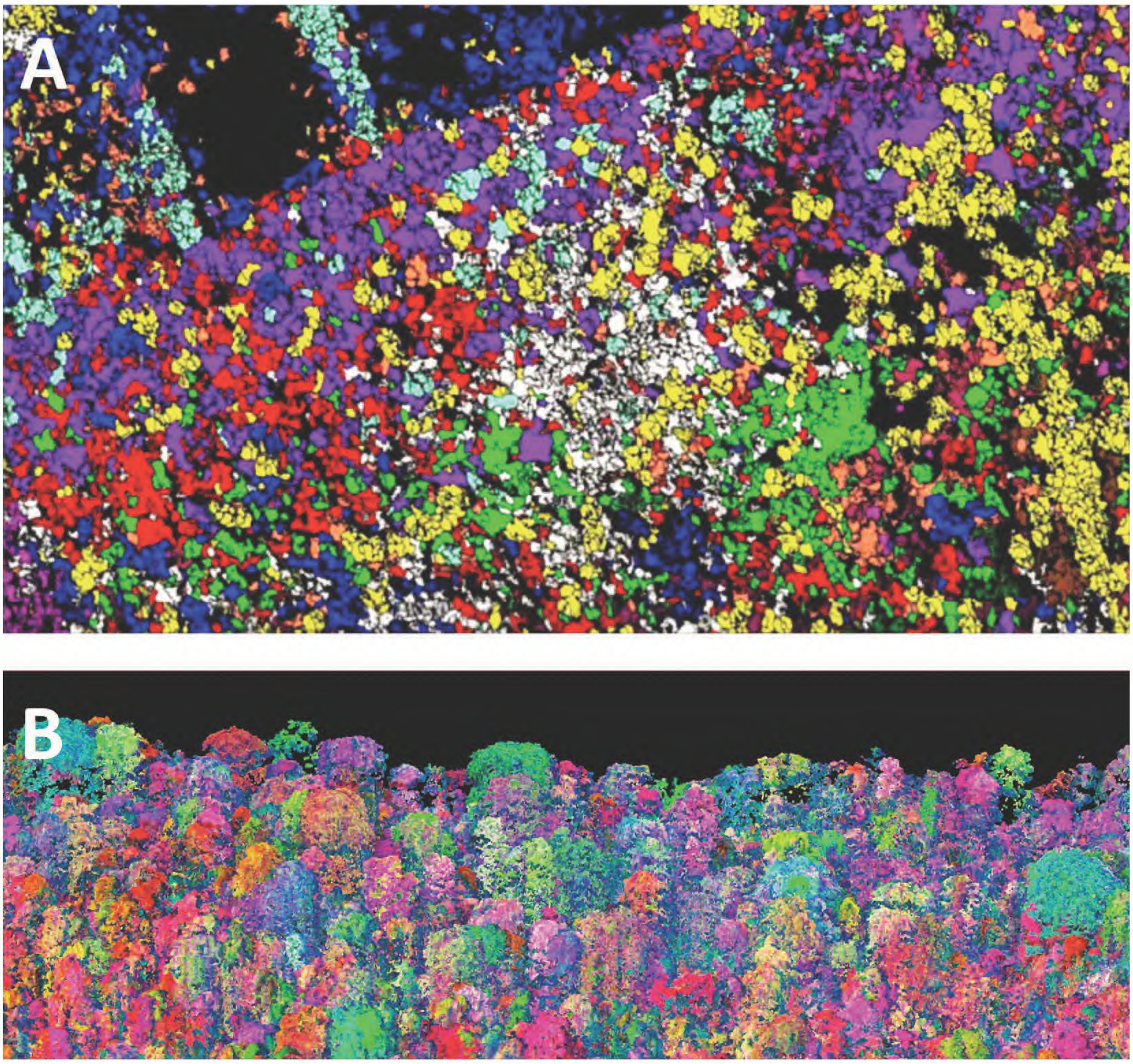


Figure 5. —A. Species classification in lowland Hawaiian tropical forest using airborne imaging spectroscopy. Black indicates non-forest areas. Each color represents a different species (Féret & Asner, 2011). —B. Structural, functional, and biological diversity in three dimensions as imaged by the Carnegie Airborne Observatory (CAO; <http://cao.ciw.edu>). This oblique view shows an Amazon rainforest canopy with colors indicating relative differences in the concentrations of growth, longevity, and defense chemicals among co-exiting canopies.

the degree to which the remotely sensed traits of an organism are unique to a given species on the landscape or within the ecosystem. Examples producing local uniqueness might include: (1) a nitrogen-fixing species (high foliar nitrogen, low LMA) against a community of non-fixers (lower nitrogen, higher LMA); (2) a bamboo species (tall, narrow open crowns, low LMA) against a community of tree canopies (wide, interlocking crowns, higher LMA); (3) light-demanding species (low LMA, low phenols/lignin) against a community of shade-tolerant species (high LMA, phenols or lignin), and so on. One of the keys to predicting which, if any, species might be unique on a landscape rests in understanding the traits among co-existing organisms. If the traits differ enough, then the species will be discernible; however, today we have a poor understanding of how many and under which conditions species might be discriminated.

What we do know comes from very recent studies at leaf and canopy scales. Asner and Martin (2009) first proposed that leaf spectra, once converted appropriately to chemical data, could be used to assess tropical forest compositional differences. This approach was extended to the canopy scale, both in modeling (Asner & Martin, 2008) and applied (Asner et al., 2008b, 2008c) work. Through this effort, it became clear that there almost always exists a set of species that can be classified from "organismic-resolution" spectrometer imagery such as is available

from the Carnegie Airborne Observatory (CAO; <http://cao.ciw.edu>). More recently, Féret and Asner (2012a) developed species classifications of humid tropical forest canopies using the spectral information measured by the CAO (Fig. 5A). This work has been nicely complemented by similar work in Costa Rican rainforests (Clark et al., 2005) and in several studies dealing with sub-tropical and temperate systems (e.g., Townsend & Foster, 2002; Bunting & Lucas, 2006; Lucas & Carter, 2008).

A case in point of species detection in tropical forests lies in the body of work focused on invasive rainforest species in the Hawaiian Islands. Detection and mapping of invasive species are key components of conservation and management efforts in Hawai'i, but the spectral and chemical separability of native, introduced, and invasive species had not been established until recently. Using organismic scale airborne imaging spectroscopy, Asner et al. (2008b) first identified the canopy spectral reflectance properties of seven common native and 24 introduced tree species, the latter group containing 12 highly invasive species. Spectral signatures of Hawaiian native trees were found to be almost universally unique from those of invasive trees and highlighted fundamental differences in the underlying canopy chemistry between the two groups. After the spectral and chemical signatures of native and invasive tree species were identified, Asner et al. (2008c) used the CAO to search for these species throughout a series of lowland to montane Hawaiian rainforests. The CAO combines imaging spectrometers with LiDAR, yielding three-dimensional spectral and structural maps that can be readily interpreted (Fig. 5B). The combined LiDAR-spectroscopic analysis highlighted the location and fractional abundance of invasive tree species throughout the forests, with field validation indicating $< 7\%$ error in the detection of invasive species with a canopy area of at least 7 m^2. This effort suggested that spectral and chemical signatures can be determined for species, which subsequently can be used to map them in airborne (and maybe someday, space-based) imagery. As a result of the Hawaiian studies, the Spectranomics Project (<http://spectranomics.ciw.edu>) was founded to inventory and analyze spectral and chemical signatures of thousands of canopy species throughout the world's tropical forests. To date, the Spectranomics Project has collected, measured, and catalogued more than 12,000 tropical forest canopy trees and lianas and is providing the baseline data for converting spectral signatures from the CAO and other airborne systems to chemical and biological diversity information (Asner et al., 2009c, 2011c, 2012b; Doughty et al., 2011; Colgan et al., 2012; Somers et al., 2012).

Finally, functional diversity (defined here as the spatial variance in functional traits among co-existing organisms) has increasingly been the focus of attention in remote sensing (Ustin & Gamon, 2010; Ollinger, 2011). One goal has centered on understanding spatial and temporal patterns of functional variance, with the intention of interpreting patterns in the context of ecological feedbacks, biogeochemical cycles, and evolutionary processes (Aguiar et al., 1996; Estes & Loveland, 1999). In tropical forests, functional diversity mapping has been difficult to put into practice, but field-based results already suggest that functional diversity is linked to gradients in soil fertility and climate (Townsend et al., 2007, 2008; Wright et al., 2007; Fyllas et al., 2009; Malhado et al., 2009; Girardin et al., 2010). In lowland Amazonian forests, Asner and Martin (2011) and Asner et al. (2014) recently extended this understanding into the remote-sensing arena by showing that a shift in canopy chemical traits, including those related to growth (e.g., phosphorus) and defense (e.g., phenols), is directly expressed in the spectral reflectance properties of the canopies. Yet, despite the systematic shift in both spectral and chemical traits, diversity among these traits within a community on a common soil type remains foremost dominated by taxonomy. That is, taxonomic control over chemical and spectral traits persists at the community level despite any synoptic-scale change in fertility conditions. More work is needed here to address the relative importance of environmental and phylogenetic contributions to functional patterns in tropical forests as detected using organismic-resolution remote sensing. The pay off from additional study will be a vastly improved understanding of biodiversity patterns and their underlying ecological and evolutionary drivers.

Macroscale Tropical Botany and Plant Ecology?

When conducting field work in the tropics, it does not take long to recognize the extreme challenges in carrying out ground-based carbon inventory, finding new species, or understanding spatial and temporal changes in community composition. Field botanists and ecologists have led the way thus far, yet there is much more to do, and field work alone will likely not yield the data required to make the scientific breakthroughs or conservation advances needed at the macroscale. Yet, remote sensing will not replace the critically important role that field botany and ecology plays in identifying species and studying their distributions in tropical forests. Rather, remote

sensing should be seen as a technique that will eventually extend our view of tropical forest carbon stocks and floristic composition to scales that are intractable on the ground. How far will remote sensing go in this realm? The answer is based on at least three factors, each requiring much more research and development: (1) the correlation between phylogenetic diversity and plant chemical and structural traits; (2) the connections between plant traits and remotely sensed variables; and (3) the development and deployment of new remote-sensing technology to support plant trait mapping and diversity assessments. Continuing progress on all three fronts will provide a pathway forward as we seek the botanical and ecological patterns needed to improve our understanding of processes operating in tropical forests at various temporal and spatial scales. The necessary information is currently difficult to obtain, but it remains key to conservation planning, forest management, and resource policy development in this century of enormous environmental change.

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